

MANGROVE SHORELINE FISHES OF BISCAYNE BAY, FLORIDA

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ABSTRACT

Biscayne Bay is a shallow subtropical lagoon on Florida's southeastern coast that is bordered to the west by the mainland and to the east by barrier islands and keys. Fish assemblages inhabiting two types of mangrove-lined shoreline that encompass the Bay were examined using a visual 'belt-transect' census method over four consecutive seasons. Several significant differences were evident between shoreline habitats in terms of fish species composition, taxonomic richness and taxon-specific densities; seasonal changes and fish size-structure differences were few. The mangrove shorelines along the mainland (ML) consistently harbored less fish taxa than those on the leeward side of the islands and keys (LK), but harbored higher densities of several euryhaline forms (i.e., killifishes and livebearers). Densities of fishes that are typically associated with coral reef habitats (i.e., snappers and grunts) tended to be higher within LK vs ML mangrove shorelines, but there were exceptions (e.g., great barracuda, *Sphyrna barracuda*). For five fish species, length-frequency distributions were compared between the Bay's mangrove shorelines and nearby coral reef habitats. These data comparisons lent partial support to an ontogenetic 'mangrove-to-reef' migration model for only two of the five species examined. Results suggest that these shoreline habitats play varying ontogenetic and trophic roles, depending on location, season and fish species. Biscayne Bay's mangrove shoreline fish assemblages appear to reflect: (1) proximity of the mangroves that they occupy to offshore reef habitats; (2) salinity regime along the shoreline; and (3) water depths within the mangrove forest interior. The fish assemblage information collected here may serve as a 'baseline' in future assessments of fishing impacts or the effects of other anthropogenic changes to Biscayne Bay and its watershed.

Mangrove habitats continue to be modified, degraded or destroyed in the southeastern U.S. and throughout tropical and subtropical ecosystems worldwide (Lewis et al., 1985; Thayer et al., 1987; Chong et al., 1990; Strong and Bancroft, 1994; Halliday and Young, 1996; Spalding et al., 1997). While marine seagrass beds are generally accepted as fish nurseries (Carr and Adams, 1973; Ogden and Zeiman 1977; Weinstein and Heck, 1979; Brothers and McFarland 1981; Martin and Cooper 1981; Robblee and Zieman 1984; Orth et al., 1984), the inherent difficulty of sampling within mangrove prop-roots has hindered our understanding of the role(s) that these habitats play in the lives of fishes. Only recently have researchers attempted to quantify fish utilization of these habitats (e.g., Thayer et al., 1987; Laegdsgaard and Johnson, 1995; Ley et al., 1999; Lorenz, 1999). Where quantitative studies have been conducted, most emphasis has been placed on revealing temporal patterns at a limited number of locations (e.g., Thayer et al., 1987; Rooker and Dennis, 1991; Laroche et al., 1997; Lin and Shao, 1999), rather than on examining how fish diversity, species-specific abundance and size-structure vary over broad spatial scales.

Biscayne Bay is a shallow, subtropical lagoon on Florida's southeastern coast that has lost some 80% of the mangrove wetland habitats that once encompassed it (Teas et al., 1976; Harlem, 1979; Snedaker and Biber, 1996). Compared to its benthic communities (i.e., seagrass and hard bottom), the Bay's mangrove habitats and the fauna that inhabit them have received virtually no attention. Consequently, although several fish species

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known to occur in Biscayne Bay seagrass beds as early juveniles (Campos, 1985; Serafy et al., 1997) have been characterized as making "ontogenetic migrations" to offshore coral reefs via mangrove habitats (Sedberry and Carter, 1993; Ogden, 1997; Ley and McIvor, 2002), the linkage between mangroves and offshore reefs in these fishes has not been examined. The present study investigated fish use of the natural shorelines of subtropical Biscayne Bay, Florida, which are lined predominantly by red mangrove (*Rhizophora mangle*). Our main objective was to compare fish utilization of prop-root habitats along the mainland with that along the leeward side of Key Biscayne, a barrier island (Hoffmeister, 1974), and the northernmost islands of the Florida Keys (i.e., Sands, Ragged and Elliot Keys). We examined spatial and seasonal differences in fish taxonomic composition and as well as variation in fish taxonomic richness (i.e., number of taxa per unit area), abundance and size-structure of the numerically dominant taxa that occupy Biscayne Bay's mangrove shorelines. We also compared the density and size-structure of selected fish taxa in mangrove versus coral reef habitats by analyzing unpublished data (described by Bohnsack et al. 1999) and by examining other data in the published literature.

METHODS

STUDY AREA.—Biscayne Bay is approximately 65 km in length, up to 15 km wide and averages 2 m deep, except in dredged channels where it can be considerably deeper (Roessler and Beardsley, 1974). Traditionally, Biscayne Bay has been considered as two connected, but structurally different, entities (e.g., de Sylva, 1976; Campos, 1985; Brand et al., 1991) with Rickenbacker Causeway serving as the north-south dividing line. Encompassed by the highly-urbanized metropolis of Miami, northern Biscayne Bay is the most altered; virtually all of its once mangrove-lined shoreline has been replaced by vertical concrete seawalls or limestone boulders. In contrast, southern Biscayne Bay has experienced much less drastic watershed and shoreline modification such that most of its perimeter is still lined with a narrow coastal band of red mangrove (Teas, 1976). The present study was conducted entirely in southern Biscayne Bay between latitudes 25° 46' N and 25° 23' N (Fig. 1).

FISH SAMPLING.—Fish assemblages were characterized and quantified using a modification of the visual 'belt-transect' census method of Rooker and Dennis (1991). This entailed snorkeling 30 m-long transects parallel to the shore and recording the identity, number, and size-structure (minimum, mean and maximum total length) of fishes observed. Measured landward from the prop-root edge, belt-transect width was 2 m, thus area censused per transect was 60 m². All visual surveys were conducted between 09:00 and 17:00 to minimize problems of low light. Censuses were conducted during consecutive wet and dry seasons (i.e., July to September and January to March, respectively). Transect locations were chosen at random each season following the method of Diaz (2001). Although a variety of sources were used to identify fish to species, especially Lindeman (1986), Robins and Ray (1986), Böhlke and Chaplin (1993), Richards et al. (1994) and Humann (1994), identification of all individuals to the species level was not possible. Rooker and Dennis (1991) articulated well the problems of visually identifying fish with highly uniform coloration and close morphology and of quantifying the constituents of large, mobile, mixed-species, schools of up to tens of thousands individuals. Therefore, following Rooker and Dennis (1991), we identified problematic taxa to the genus or family level (e.g., *Eucinostomus*, Scaridae) and following Humann (1994), we placed into a single group all small, silvery, fork-tailed fishes that tend to inhabit the water-column in large schools (e.g., Engraulidae, Atherinidae and Clupeidae). The latter group is henceforth referred to as small, water-column fishes.

MICROHABITAT MEASUREMENTS.—Measurements of water quality and depth were obtained for each fish census. Water temperature, salinity and dissolved oxygen were measured using a Hydrolab® multi-probe instrument. Depth was measured along (i.e., at 0, 15 and 30 m) each transect using a 2

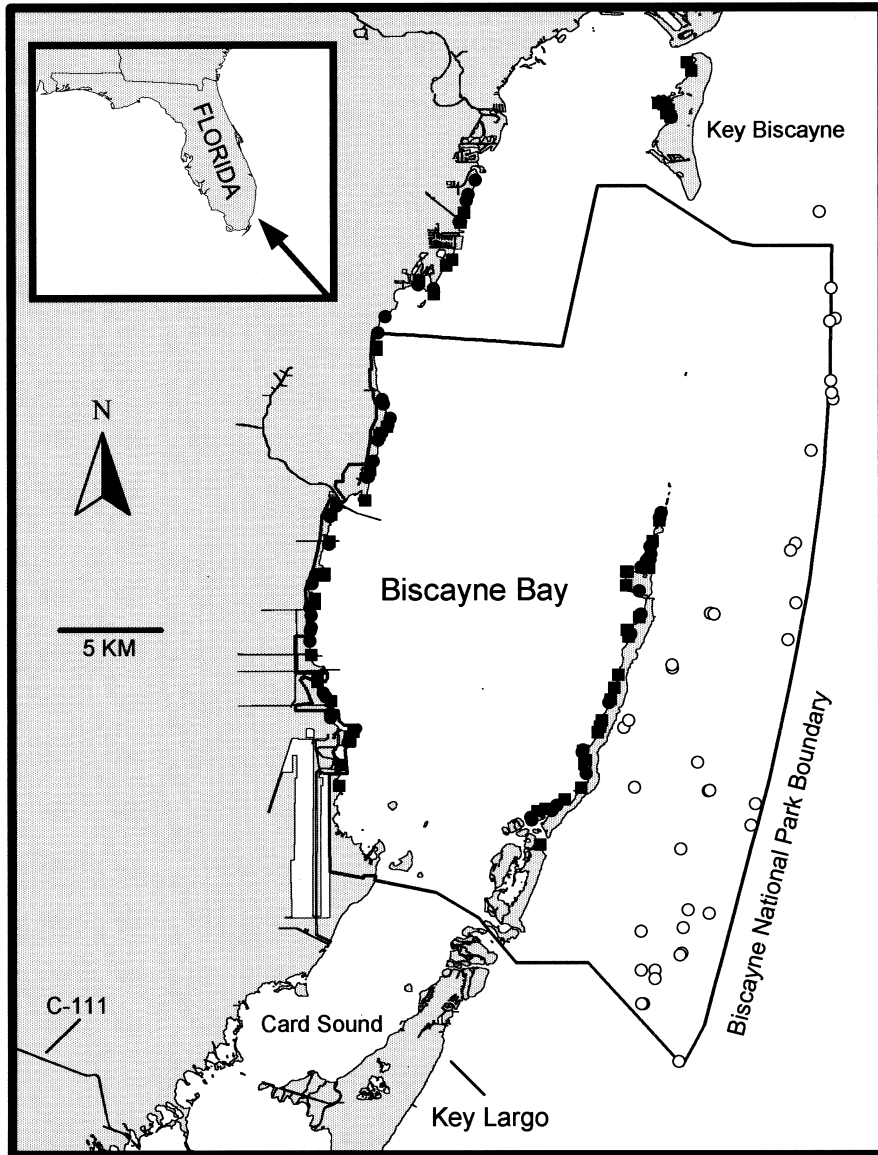


Figure 1. Location of Biscayne Bay on Florida's (USA) coastline (inset) and a map depicting the location of visual fish censuses (1998 to 2000). Shaded circles (dry season) and squares (wet season) indicate visual transect locations on the mainland and leeward shorelines on the leeward side of the islands (keys) that rim Biscayne Bay. Open circles indicate visual fish census locations performed by Bohnsack et al. (1999) over reef habitats. Solid line indicates the boundary of Biscayne National Park.

m-long polyvinyl chloride pole marked off every 2 cm. In a separate effort, a subset of the fish census sites (mainland, $n = 27$; leeward key, $n = 22$) were selected randomly (i.e., using a random number table) and re-visited to obtain density and diameter measurements of prop-roots as well as an index of epibiont coverage on the roots (i.e., measured as the maximum diameter of the attached organism assemblage). Prop-root density and diameter measurements followed Thayer et al. (1987). The former was measured by counting the number of roots within three 1 m^2 quadrats (i.e., at 0, 15

and 30 m) and the latter by measuring with vernier calipers the maximum width of roots (and roots plus epibionts) within the above quadrats.

DATA ANALYSES.—The present study was designed to compare fish assemblages associated with two mangrove shoreline types. The two shorelines correspond to those described by Lindeman et al. (1998): mangrove shorelines along the mainland (ML) and those on the leeward side of the major keys (LK) that constitute much of the Bay's eastern boundary (i.e., Key Biscayne, Sands Key, Ragged Keys and Elliot Key; Fig. 1). Our null hypotheses were that, regardless of season, these two mangrove shoreline types harbored essentially the same fish species, were equally diverse (i.e., rich in taxa, hereafter termed taxonomic richness) and that taxon-specific density and size-structure differences between shorelines were minor. Taxonomic richness was the number of different taxa observed per transect. Variations in taxonomic richness and in the densities of 'dominant taxa' were analyzed using SAS (1990) computer software. The criteria for a given taxon to be designated as dominant was that: (1) it must have occurred in at least 30% of all censuses; and (2) its overall abundance (total number observed) was greater than one percent of the total numbers of fishes counted.

Prior to statistical analyses, data were screened as to whether they met the assumptions of normality and equal variance. If so, analysis of variance (ANOVA) models were employed to test for: (1) shoreline differences (i.e., ML versus LK) within each season (i.e., Wet '98, Dry '99, Wet '99 and Dry '00); and (2) seasonal differences within each shoreline type. The above was achieved by first applying 'full' ANOVA models with the factors shoreline type, season and the interaction term. In the event that the interaction term was found non-significant (i.e., $P > 0.05$) it was removed and the model re-run until all terms were significant (Draper and Smith 1981). If, even after transformation, the normality and equal variance assumptions could not be met, non-parametric Kruskal-Wallis tests were performed on rank scores.

Relationships between microhabitat measures and fishes (i.e., fish taxonomic richness and taxon-specific fish densities) were examined graphically and by correlation analyses. Specifically, the strength and direction of fish-microhabitat relationships were assessed from the magnitude of Pearson correlation coefficients or Spearman rank correlation coefficients, depending on the distribution of variable in question (Zar, 1984). Only statistically significant ($P < 0.05$) correlation coefficients with absolute values exceeding 0.50 were considered potentially meaningful.

Length-frequency (percent) distributions with 1, 5 or 10 cm intervals (depending on fish sizes) were constructed and compared for the dominant fish taxa at ML and LK shorelines by applying the technique used by Ault et al. (1998) which is fully detailed by Meester et al. (1999). This technique generates taxon-specific, size-frequency data for each census by: (1) assuming a normal density distribution about the mean size observed; and (2) using the minimum and maximum sizes observed to define the upper and lower tails of the above normal distribution (see Meester et al., 1999). Following Ley et al. (1999), literature values of minimum length-at-maturity, when available, were indicated on each length-frequency plot to reveal the life-stage(s) utilizing ML and LK mangrove shorelines and to generate mature:immature proportions. Sources used for length-at-maturity information were Hardy (1978), Monro (1983), Thresher (1984) and Claro (1994). In addition, length-frequency data for those species that also occur in the coral reef habitats that lie directly east of Biscayne Bay were indicated on our (mangrove shoreline) size-structure plots. The reef fish dataset examined here was an updated subset of that described previously by Bohnsack et al. (1999) for 38 reef stations censused from 1996 to 2000 (see Fig. 1).

RESULTS

A total of 129, 60 m² belt-transects were censused over four consecutive seasons, beginning with the wet season of 1998 and ending with the dry season of 2000. Sample sizes (number of censuses) ranged from 15 to 18 within each mangrove type for each

season. Thirty-eight fish taxa, belonging to 23 families of fishes, were observed (Table 1); 21 along the ML and 34 along LK mangrove shorelines. The two shoreline types shared 17 taxa. Taxa unique to ML mangrove shorelines, were two killifishes (*Fundulus confluentus* and *Lucania parva*), a drum (*Sciaenops ocellatus*) and a cichlid species (*Cichlasoma urophthalmus*). Unique to LK mangrove shorelines was diverse group of 17 fish taxa. These included one or more species of nurse shark, stingray, moray eel, jack, snapper, grunt, sea chub, surgeonfish, parrotfish, boxfish and puffer.

Statistical comparisons of fish utilization of ML versus LK mangrove shoreline habitats and season were limited to ten variables (Table 2): mean taxonomic richness and mean densities of small, water-column fishes, goldspotted killifish (*Floridichthys carpio*), gray snapper (*Lutjanus griseus*), schoolmaster (*L. apodus*), sailors choice (*Haemulon parra*), bluestriped grunt (*H. sciurus*), small mojarra (*Eucinostomus* sp.), yellowfin mojarra (*Gerres cinereus*) and great barracuda (*Sphyrna barracuda*). Untransformed taxonomic richness values met the assumptions of normality and homogeneity of variance, thus these data were analyzed with ANOVA followed by t-tests. This was not the case of any of the taxon-specific density data, even after application of a variety of data transformations suggested by Sokal and Rohlf (1987). Thus, non-parametric Kruskal-Wallis tests were performed.

Analysis of variance and t-tests indicated that mean taxonomic richness varied significantly by shoreline type only and that mean values at ML sites were significantly lower than at LK sites (Table 2). Similarly, Kruskal-Wallis tests indicated that the densities of three species (schoolmaster, sailors choice and bluestriped grunt), were significantly ($P < 0.05$) lower along ML versus LK mangrove shorelines during each of four seasons (Table 2). During all but one season, mean densities of gray snapper were significantly lower along ML versus LK shorelines. For goldspotted killifish, significant ($P < 0.01$) differences between shorelines were restricted to the dry seasons when 24-fold, or greater, mean densities were observed along ML shorelines as compared to LK shorelines. For mean densities of yellowfin mojarra and great barracuda, no significant differences between shorelines were found. Similarly, mean densities of Eucinostomid mojarra were not significantly different between shorelines during most (i.e., three of four) of the seasons examined. Mean densities of small, water column fishes followed no clear pattern: they were significantly lower along ML shorelines during one wet and one dry season, significantly higher along ML shorelines during one dry season and statistically equivalent during one wet season.

Seasonal differences in mean taxonomic richness within each shoreline type were not significant. Only three of the nine taxa examined exhibited statistically significant seasonal patterns in their respective densities and these were shoreline-specific. Greater abundance during the wet seasons was observed in schoolmaster within the LK shoreline only, and in gray snapper within the ML shoreline only. Similarly, goldspotted killifish had significantly higher densities during the dry season, but only within the ML shoreline.

Whereas water temperature, dissolved oxygen and depth at ML and LK sites were similar (Fig. 2), relatively large differences in both mean seasonal salinity and salinity variation were evident. Specifically, mean salinities at ML sites were consistently lower, varying from 20.6 to 29.3‰ each season, whereas at LK sites, means varied from 34.1 to 36.7 ppt each season. More striking was the difference in salinity range between ML and LK mangrove shorelines (Fig. 2B): ranges of up to 25.5‰ were observed at ML sites versus salinity ranges of 10.8‰ or less at LK sites. Within shorelines, mean salinity

Table 1. List of fish taxa observed via 60 m² visual belt transects along Biscayne Bay's (Florida, USA) mainland (ML) and leeward key (LK) mangrove shorelines from 1998 to 2000. SWCF = small, water column fishes (see text for details).

Family	Taxon	Common Name	Number Observed		Total Length (cm)		
			ML	LK	Total	Min.	Max.
Orectolobidae (nurse sharks)	<i>Ginglymostoma cirratum</i>	nurse shark		1	1	122	122.0
Dasyatidae (stingrays)	<i>Urolophus hamae</i>	yellow stingray		1	1	31	31.0
Muraenidae (moray eels)	<i>Gymnothorax funebris</i>	green moray		1	1	64	64.0
Clupeidae/Engraulidae/Atherinidae	herrings/anchovies/silversides	SWCF	39,488	211,834	251,322	1	4.5
Belontiidae (needlefishes)	<i>Strongylura notata</i>	redfin needlefish	13	133	146	10	18.2
Cyprinodontidae (killifishes)	<i>Cyprinodon variegatus</i>	sheepshead minnow	4	3	7	1	3.0
	<i>Floridichthys carpio</i>	goldspotted killifish	4,305	124	4,429	1	3.5
	<i>Fundulus confluentus</i>	marsh killifish	22		22	1	3.0
	<i>Fundulus sp.</i>	Unid. Fundulid	44	1	45	1	2.5
	<i>Lucania parva</i>	rainwater killifish	24		24	1	3.0
Poeciliidae (livebearers)	<i>Poecilia latipinna</i>	salfin molly	105	25	130	1	4.5
Centropomidae (snooks)	<i>Centropomus undecimalis</i>	snook	17	2	19	61	84.4
Carangidae (jacks)	<i>Caranx ruber</i>	bar jack		2	2	31	32.0
Lutjanidae (snappers)	<i>Lutjanus analis</i>	mutton snapper		1	1	64	64.0
	<i>Lutjanus apodus</i>	schoolmaster	14	286	300	4	11.8
	<i>Lutjanus griseus</i>	gray snapper	246	1,630	1,876	4	16.2
Gerridae (mojarra)	<i>Eucinostomus sp.</i>	Eucinostomid mojarra	3,638	1,945	5,583	1	5.3
	<i>Gerres cinereus</i>	yellowfin mojarra	315	169	484	4	13.6
Haemulidae (grunts)	<i>Haemulon flavolineatum</i>	French grunt		303	303	8	11.9
	<i>Haemulon parra</i>	sailors choice	7	402	409	3	10.3
	<i>Haemulon plumieri</i>	white grunt		2	2	10	10.0
	<i>Haemulon sciurus</i>	bluestriped grunt		707	707	4	12.2
	<i>Haemulon sp.</i>	Unid. Haemulid		4	4	3	8.7
Sparidae (porgies)	<i>Lagodon rhomboides</i>	pinfish	33	8	41	8	11.1
Sciaenidae (drums)	<i>Sciaenops ocellatus</i>	red drum	1		1	66	66.0
Kyphosidae (sea chubs)	<i>Kyphosus sectatrix</i>	Bermuda chub		21	21	8	15.7
Cichlidae (cichlids)	<i>Cichlasoma urophthalmus</i>	Mayan cichlid	6		6	8	10.0
Pomacentridae (damselfishes)	<i>Abudefduf saxatilis</i>	sergeant major	4	103	107	1	7.2
Mugilidae (mullets)	<i>Mugil cephalus</i>	striped mullet	50	10	60	18	31.0
Sphyraenidae (barracudas)	<i>Sphyraena barracuda</i>	great barracuda	89	125	214	5	25.4
Acanthuridae (surgefishes)	<i>Acanthurus coeruleus</i>	blue tang		1	1	8	8.0
Scaridae (parrotfishes)	<i>Scarus guacamaia</i>	rainbow parrotfish		62	62	10	17.0
	<i>Scarus/Sparisoma sp.</i>	parrotfish		88	88	8	14.4
Ostraciidae (boxfishes)	<i>Sparisoma viride</i>	stoplight parrotfish		1	1	13	13.0
	<i>Lactophrys triqueter</i>	smooth trunkfish		2	2	15	17.5
	<i>Lactophrys sp.</i>	Unid. cowfish		1	1	28	28.0
Tetraodontidae (puffers)	<i>Diodon hystrix</i>	porcupinefish		1	1	61	61.0
	<i>Spheroides testudineus</i>	checkered puffer	31	7	38	3	11.0

Table 2. Comparisons of fish taxonomic richness (number of fish taxa per unit area) and the densities of nine dominant fish taxa observed along mainland (ML) versus leeward key (LK) mangrove shorelines of Biscayne Bay, Florida, USA. Values are means per transect (60 m²). Analysis of variance followed by t-tests was conducted to compare mean fish taxonomic richness values. For taxon-specific density comparisons, non-parametric Kruskal-Wallis tests were performed. One, two or three asterisks indicate statistical significance at the $P < 0.05$, $P < 0.01$ and $P < 0.001$ levels, respectively. ns = not significant.

	Wet 1998			Dry 1999			Wet 1999			Dry 2000		
	ML	LK	p	ML	LK	p	ML	LK	p	ML	LK	p
n	15	17		17	15		15	18		16	16	
Taxonomic richness	3.27	8.71	***	3.59	7.20	***	4.53	7.50	*	3.63	6.25	**
Clupeidae/Engraulidae/Atherinidae	390.60	9,014.71	**	819.24	652.87	*	763.47	1,595.06	ns	328.13	1,255.00	**
goldspotted killifish	0.00	0.82	ns	137.24	5.53	**	3.73	1.39	ns	119.75	0.13	***
gray snapper	6.20	23.12	*	0.35	23.80	**	8.13	19.44	ns	0.06	33.13	***
schoolmaster	0.60	6.06	***	0.00	2.20	***	0.33	7.78	***	0.00	0.63	*
Eucinostomid mojarra	17.27	33.77	ns	152.12	30.93	ns	15.33	29.67	*	34.38	23.31	ns
sailors choice	0.00	4.65	***	0.41	6.07	***	0.00	6.39	***	0.00	7.31	**
bluestriped grunt	0.00	11.65	**	0.00	7.00	**	0.00	8.50	***	0.00	15.69	***
yellowfin mojarra	8.13	2.53	ns	6.88	2.00	ns	4.27	3.33	ns	0.44	2.25	ns
great barracuda	2.13	2.71	ns	1.24	1.00	ns	1.80	2.39	ns	0.50	1.31	ns

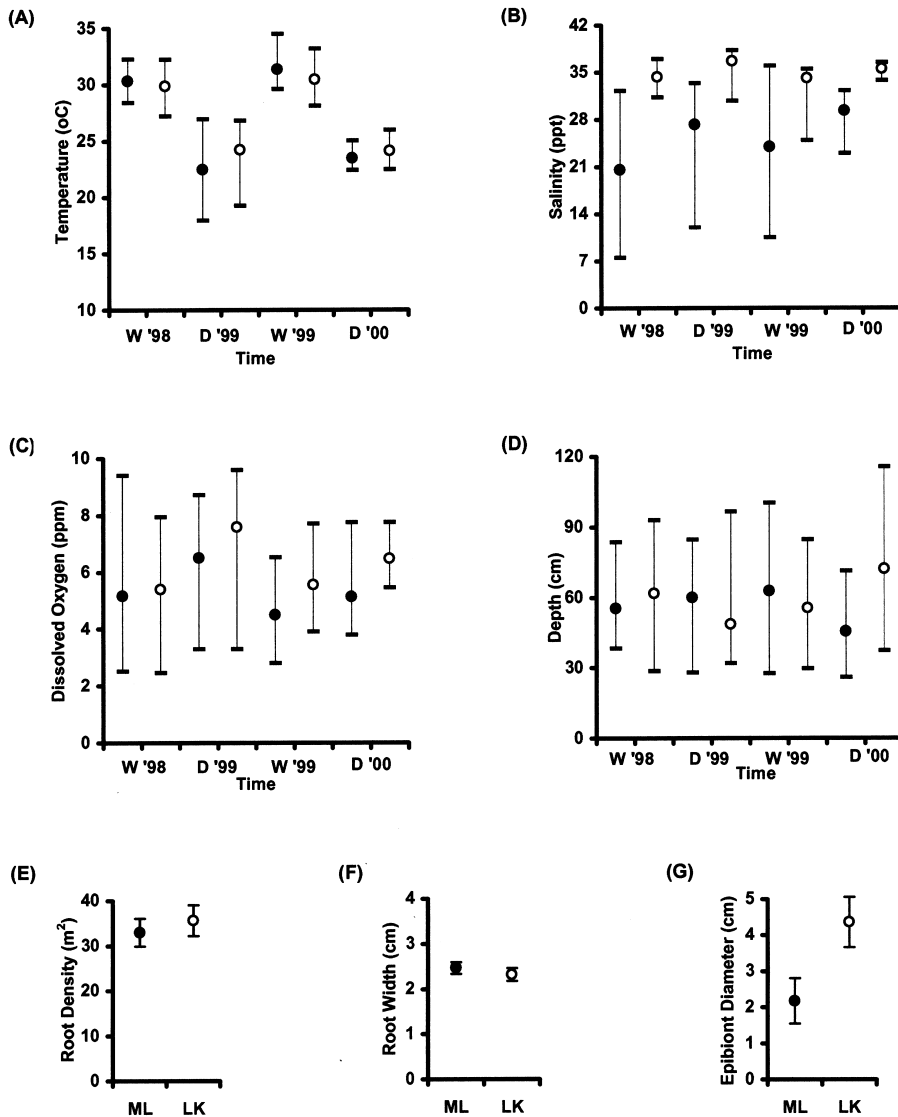


Figure 2. Microhabitat variables measured along Biscayne Bay (Florida, USA) mangrove shorelines of the mainland (ML, black circles) and the leeward side of the keys (LK, open circles). For water temperature, salinity, dissolved oxygen and depth (A–D) minima, mean and maxima are shown for each season. For mangrove density, root diameter and quantities of attached epibionts, overall means (± 1 SE) are shown. For (A–D) each data point and error bar is based on sample sizes (n) of 15 to 18 measurements per season; for (E–F) $n = 27$ and 22 , for ML and LK, respectively.

tended to be lower during the wet versus the dry season, with the smallest seasonal differences along the LK shoreline — a consequence of the relatively small watersheds upstream of LK sites and their closer proximity to the open, high-salinity waters of the Atlantic Ocean. The ML and LK shorelines were characterized by similar prop-root densities and root diameters (Fig. 2E,F), however, our index of attached epibiont coverage

on LK prop-roots averaged twice that of ML prop-roots (Fig. 2G). All correlations between microhabitat measures and fishes (i.e., fish taxonomic richness and taxon-specific densities) were weak. The only statistically significant correlation coefficients with absolute values greater than 0.50 were positive relationships between salinity and the densities of schoolmaster, bluestriped grunt and sailors choice. Corresponding Spearman rank correlation coefficients for the above salinity versus density relationships were +0.502, +0.557 and +0.512, respectively.

Comparison of the size structures of the dominant taxa revealed more similarities than differences for fishes inhabiting ML versus LK shorelines (Fig. 3). For example, modal lengths for goldspotted killifish, gray snapper, schoolmaster, yellowfin mojarra and great barracuda were essentially the same for both shorelines, although there was a tendency for LK shorelines to harbor larger gray snapper, yellowfin mojarra and great barracuda than ML shorelines. The greatest difference between shorelines was in their respective size-structures of Eucinostomid fishes. The ML shorelines were dominated by individuals ranging from 2 to 6 cm TL, whereas in LK shorelines, they tended to be larger, with the ≥ 6 cm size-classes constituting 9% of those observed at ML versus 60% of those observed at LK shorelines. The rarity of sailors choice ($n = 7$) and the absence of bluestriped grunt in ML censuses, precluded meaningful size-structure comparisons for these species.

Minimum size-at-maturity information was found in the literature for five of the nine taxa examined: gray snapper, schoolmaster, yellowfin mojarra, bluestriped grunt and great barracuda (Fig. 3). For two species, goldspotted killifish and sailors choice, we considered sheepshead minnow (*Cyprinodon variegatus*) and bluestriped grunt, respectively, as 'surrogates' and used their reported values. Examination of mature:immature proportions suggested that: (1) the goldspotted killifish and gray snapper observed were mostly mature (i.e., 0.76 and 0.80, respectively); (2) the schoolmaster, sailors choice and great barracuda were mostly immature (i.e., 0.10, 0.19 and 0.06, respectively); and (3) the shorelines harbored approximately equal proportions of mature and immature stages of yellowfin mojarra and bluestriped grunt (i.e., 0.46, and 0.48, respectively).

Six of our 'dominant' mangrove fishes were also found in coral reef habitats directly east of Biscayne Bay, but, for length-frequency plots, an adequate number of observations existed for only five (Fig. 3): gray snapper, schoolmaster, sailors choice, bluestriped grunt and great barracuda. Comparison of each species' size-frequency distribution in mangrove versus coral reef habitats suggested that, in general, schoolmaster and great barracuda followed the ontogenetic 'mangrove-to-reef' migration model. The proportion of mature schoolmaster in Biscayne Bay mangroves was 0.10 vs 0.56 on nearby reef habitats; corresponding proportions for great barracuda were 0.06 and 0.53. In contrast, modal length of gray snapper in offshore reef habitats was one (5 cm) size-class less than that observed along Biscayne Bay's mangrove shorelines, with the proportion of mature individuals estimated as 0.50 on the reefs versus 0.80 in the mangroves. The length-frequency distributions of bluestriped grunt and sailors choice were essentially the same in mangrove and coral reef habitats.

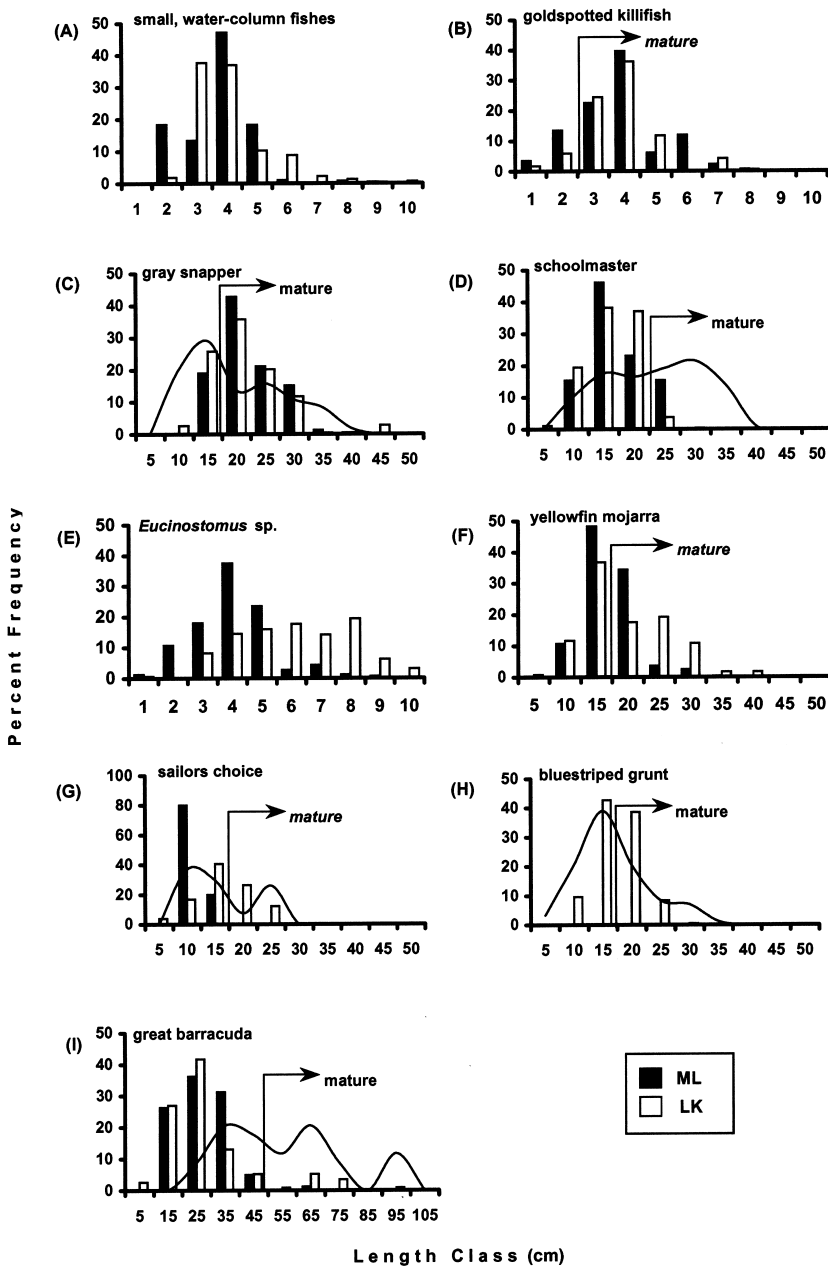


Figure 3. Percent length-frequency plots for nine dominant fish taxa observed in mangrove shorelines along the mainland (ML, black bars) and those long the leeward side of the keys (LK, open bars) of Biscayne Bay, Florida, USA. Solid lines indicate size structure of taxa (for which length-frequency data was available) on adjacent reef habitats (see Bohnsack et al., 1999 for details). Vertical lines (with arrows) indicate minimum size-at-maturity values obtained from the literature. Refer to Table 1 for sample sizes (i.e., number of fish) for ML and LK shorelines. Sample sizes for fishes observed in adjacent reef habitats are: (C) 1132 gray snapper; (D) 574 schoolmaster; (G) 29 sailors choice; (H) 1305 bluestriped grunt; and (I) 37 great barracuda. Small, water-column fishes include Engraulidae, Atherinidae and Clupeidae combined (see text for details).

DISCUSSION

Results suggest that underwater visual fish census is a rapid and effective technique for gathering data on the fishes that occupy Biscayne Bay's mangrove-lined shorelines and for making quantitative comparisons of fish distribution, abundance and size-structure within and among habitat types (see Tables 2,3). Visual fish census has become the most accepted method for estimating fish abundance and diversity in coral reef environments (Thresher and Gunn, 1986; Cheal and Thompson, 1997; Thompson and Mapstone, 1997). Increasingly, visual census data are being used to assess reef fish stocks (Bellwood and Alcala, 1988, Ault et al., 1998) and to understand relationships among fish assemblages, reef structure and hydrodynamic regimes (McGehee, 1994; Green, 1996; Jennings et al., 1996). Our rationale for employing visual fish census was that it was non-destructive of both mangrove habitat and fishes and that it could be performed rapidly among these rigid, complex structures that typically defy the use of conventional 'active' fish sampling techniques. Visual techniques are useless where (and when) water clarity is consistently poor, the mangroves themselves exclude human access and/or the water is extremely shallow (i.e., <10 cm). In our area, one or more of these conditions prevail along many of the mangrove-lined canals and natural creeks that empty into Biscayne Bay, and, where these areas still exist, throughout most of the mangrove forest interior habitats that are only seasonally or tidally inundated. These limitations aside, visual fish census appears to be a greatly underutilized technique for obtaining quantitative data on fish utilization of mangroves, especially in non-estuarine areas that tend to have high visibility (e.g., van der Velde et al., 1992, Claro and Garcia-Arteaga, 1993; Ley et al., 1999; Negelkerken et al. 2000). High visibility areas include much of the mangrove-lined shorelines along the mainland and keys of southeastern Florida, and analogous mangrove habitats that rim Bahamian and Caribbean waters.

Our list of 34 fish taxa differs from that of Voss et al. (1969) which is the only previous compilation of Biscayne Bay's mangrove fishes: we observed only 12 of the 57 fishes that they listed. This discrepancy likely reflects differences in sampling methods, effort and area (which are not specified in Voss et al., 1969), although the possibility that the Bay's fish assemblages have changed over the last 30 yrs cannot be ruled out. The fact that we observed the exotic Mayan cichlid (*Cichlasoma urophthalmus*) in ML mangroves, and Voss et al. (1969) did not list them, indicates that this is a relatively new species to the Bay's mangrove habitats. This species, first collected in 1983, likely spread from a source population within mangrove habitats upstream of Florida Bay (Loftus, 1987). Less clear, however, is why species of the genus *Haemulon*, which were conspicuous components of the LK shorelines that we surveyed, were not listed by Voss et al. (1969). In contrast, two Lutjanid species have clearly endured in Biscayne Bay mangroves over the last 100 yrs: gray snapper and schoolmaster. Referring to the former, Smith (1895) stated "...the fish was found in incredible numbers under mangrove trees, the shores for miles being lined by immense bodies of snappers...". Unfortunately, lack of quantitative data on the fishes of the Bay's mangrove habitats preclude historical fish abundance comparisons.

The ichthyofauna of Biscayne Bay's mangrove shorelines closely resemble that of its southern neighbor, Florida Bay, although, again, differences among studies in sampling effort, methodology and time of sampling need to be considered. Each working independently about a decade ago, Thayer et al. (1987) and Ley et al. (1999) both sampled mangrove fishes in Florida Bay using block nets and poison; Ley et al. (1999) also conducted

Table 3. Comparison of mean fish density estimates in the present study (Biscayne Bay, ML and LK mangrove shorelines combined) with those reported in other studies that also employed visual fish census techniques. Units are fish m⁻². n/r = not reported. *our calculations based on data provided by J. Bohnsack and D. Harper (National Marine Fisheries Service, Miami, Florida). **values provided by authors (i.e., Ley and McIvor, 2002).

Species	Present study		Ley and McIvor (2002)		Bohnsack et al. (1999)		Negelkerken et al. (2000)	
	Biscayne Bay mangroves	Reefs adjacent to Biscayne Bay*	Florida Bay mangroves**	Florida Keys reef tract	Bonaire mangroves	Bonaire reefs		
schoolmaster	0.0385	0.0088	0.0127	0.0064	0.0658	0.0034		
gray snapper	0.2405	0.0174	0.3625	0.0160	0.0299	0.0000		
sailors choice	0.0524	0.0004	n/r	0.0010	n/r	n/r		
bluestriped grunt	0.0906	0.0199	0.0277	0.0271	0.0043	0.0027		
great barracuda	0.0274	0.0006	0.0146	0.0015	0.0051	0.0001		

visual censuses. Thayer et al. (1987) collected 64 fish taxa from eight study locations in western Florida Bay and Ley et al. (1999) collected or observed 76 taxa from 17 locations in eastern Florida Bay. Their studies each yielded species lists that included about 60% of the species observed in the present study. Fishes present in our study, but absent from both Florida Bay mangrove studies, tended to be the reef-associated species that were either entirely restricted to, or more common within, Biscayne Bay's LK mangrove shorelines: green moray (*Gynothorax funebris*), bar jack (*Caranx ruber*), french grunt (*Haemulon flavolineatum*), Bermuda chub (*Kyphosus sectatrix*), sergeant major (*Abudefduf saxatilis*), two boxfishes (Ostraciidae) and two puffers (Tetradontidae). The above taxa likely occur in mangrove habitats along the leeward side of the keys along the eastern edge of Florida Bay, but the fishes of these habitats have yet to be documented. Until these shorelines and the mangrove habitats on the windward side of the Florida Keys have been sampled, the list of fishes occupying Biscayne Bay's LK mangrove shorelines will bear stronger resemblance to that of Rooker and Dennis (1991) for mangrove islands off Puerto Rico than to the lists compiled for Florida Bay and adjacent waters.

The main quantitative findings of our Biscayne Bay study were that: (1) the mangrove-lined shorelines along the mainland (ML) consistently harbored fewer fish taxa than those on the leeward side of the keys (LK); (2) the ML mangrove shorelines harbored higher densities of several euryhaline forms (i.e., killifishes, livebearers) than LK mangrove shorelines; (3) the LK mangrove shorelines contained significantly higher densities of fishes which are typically associated with coral reef habitats (e.g., snappers and grunts), but there were exceptions (i.e., great barracuda); (4) significant seasonal changes in density were detected in only three of the nine taxa examined; (5) fish-microhabitat measure correlations were generally weak, but of those examined, salinity was the most important; (6) fish size-structure differences between shorelines were minor; and (7) length-frequency data for only two of the five fish species for which mangrove versus reef size-structure comparisons could be made, were consistent with the 'mangrove-to-reef' ontogenetic migration model.

The simplest explanation for (1) and (2) above lies in the respective proximity (i.e., cross-shelf location, sensu Lindeman et al., 1998) of each shoreline to offshore reef habitats and/or areas characterized by wide salinity fluctuation. Fish diversity and species composition differences between mangrove shorelines likely reflect the larger 'pool' of species (at larval through adult stages) that would be expected to come into contact with LK versus ML shorelines. Wide salinity fluctuation and lower mean salinity are characteristics of ML shorelines and these may directly or indirectly reduce fish species diversity and density. Comparing juvenile fishes inhabiting Biscayne Bay seagrass beds that were exposed to wide versus narrow salinity variation, Serafy et al. (1997) found lower species richness and lower densities of reef-associated juveniles at sites that were frequently exposed to pulses of fresh water discharged by the coastal canal system. Our finding in the present study of substantially greater amounts of attached epibionts on LK versus ML prop-roots is likely related to the lower salinity variation at the former. Attached epibiont communities are known to harbor abundant invertebrate species (Laegdsgaard and Johnson, 2001) which, in turn, represent important prey for many of the fishes we observed (Ley et al., 1994). Thus, shoreline fish differences may reflect the availability and/or the salinity tolerance of the algal-invertebrate community attached to the prop-roots as much as the physiological capabilities and water quality preferences of the fishes themselves.

While we can probably ascribe most of the species-specific fish density differences between shorelines to their location, fish habitat preferences and salinity tolerances of the community, other factors may actually drive the patterns of distribution and abundance that we observed. For example, it is likely that the consistent pattern of very high densities of goldspotted killifish along ML shorelines during the dry season followed by very low densities during the wet season was due to seasonal differences in water levels in the mangrove forest interior, i.e., conditions in a habitat outside our sampling domain. Specifically, we suspect that each dry season individuals of this species were seasonally 'forced' by receding water levels from the forest interior to the forest perimeter—a location where the predation risk is probably high and food resources increasingly depleted as conspecifics and other small fishes concentrate (Lorenz, 1999, 2000). If this mechanism is indeed operating, this example serves as a caveat to those using high animal density as a proxy for high habitat quality in 'essential fish habitat' studies (*sensu* NOAA, 1996). Wave energy is another factor that may influence mangrove communities and/or the distribution and abundance of their component taxa. Unfortunately, we have no data to correlate wave energy levels with our results.

While adequate for making relative, within-study comparisons using rank scores, the absolute densities of small, water-column fishes reported in the present study are questionable. Because this group of fishes often occurred in such large schools as to overwhelm the observer's ability to enumerate them, a technique other than visual census needs to be considered to quantify, let alone identify to species, this potentially important assemblage component.

Gray snapper and schoolmaster were the only fish taxa, other than goldspotted killifish, for which we detected significant seasonal density changes: both had higher densities during the warm, wet season than in the cool, dry season. In terms of seasonal density differences, our results differ somewhat from those of Rooker and Dennis (1991). They found no seasonal differences in density for gray snapper or schoolmaster, but detected significant (wet-dry) seasonal differences for bluestriped grunt, sailors choice, yellowfin mojarra, and eucinostomids. These differences may reflect differential patterns of habitat use under subtropical (Biscayne Bay) vs tropical (Puerto Rico) conditions.

Many reef fish species have been described as making ontogenetic migrations from seagrass to mangrove to reef habitats (Odum et al., 1982; Ogden and Gladfelter, 1983; Gilmore and Snedaker, 1993; Sedberry and Carter, 1993; Ogden, 1997). Bardach (1959) was among the first to suggest that the persistence of the extraordinarily high levels of fish density, biomass and diversity on reefs was largely due to the reef's connection with adjacent seagrass and mangrove systems. Parrish (1989) reviewed interactions between reef fish communities and shallow-water habitats. He conjectured that reefs represent a limited and difficult target for planktonic fish larvae to 'hit' and that settling in nearby habitats and then migrating to reefs later in life may be the preferred strategy among several taxa (Parrish 1989). Given the literature above, we expected that our length-frequency comparisons would show modal size progression from mangrove to reef for each of the five reef-associated fishes examined. While this exercise yielded results consistent with the 'mangrove-to-reef' ontogenetic migrations for schoolmaster and great barracuda, those for gray snapper and the two grunts were not. There are at least three explanations for the above findings that are not mutually exclusive.

The first reason is that fishing pressure on the reef exceeds that in the mangrove habitats and that reef fishers retain gray snapper, bluestriped grunt and sailors choice over

schoolmaster and great barracuda. Consequently, the largest size-classes of gray snapper and the two grunts do in fact migrate from mangrove to reef, but are so quickly harvested, they are rarely observed in reef fish censuses. Data to evaluate this scenario do not exist, mainly because the fishing practices and impacts within the two habitats have not been studied separately. However, a recent report on the fish populations occupying the reef habitats of Biscayne National Park (BNP) suggested that both snappers, bluestriped grunt and great barracuda (but not sailors choice) are overexploited (Ault et al., 2001). Harper et al. (2000), who analyzed creel survey data from a dock within BNP, reported data indicating that retention rates (percentage of fish landed versus released) for each of the five species ranged from 63 to 88%, with the lowest corresponding to great barracuda and the highest schoolmaster. Only one study has reported on possible fishing impacts on gray snapper in Biscayne Bay proper (i.e., its inshore waters). Faunce et al. (2002) compared gray snapper length-frequencies in mangroves of northern Florida Bay, southern Biscayne Bay and in an area closed to human access (and therefore, fishing) for the protection of American crocodile (*Crocodylus acutus*). While the modal sizes of fish in Biscayne and Florida Bays were each at 15–20 cm TL, that within the unfished crocodile sanctuary was two size-classes greater at 25–30 cm TL. Directed study of fishing effects on Biscayne Bay's fish populations during their occupation of inshore waters is recommended.

The second possible reason for a lack of ontogenetic migration pattern is that some proportion of mature and immature gray snapper, bluestriped grunt and sailors choice do not so much 'shift' in ontogenetic sequence from mangrove to reef habitats as much as they 'expand' into these areas. This scenario, whereby individuals essentially incorporate more and more habitats in their repertoire as they grow, would also produce the substantial size-structure overlap among mangrove and reef habitats that was apparent for all five of the species examined here. In their comparison of fish use of seagrass, mangrove and reef habitats off Bonaire, Negelkerken et al. (2000) obtained similar results in their analysis of the length-frequencies of gray snapper, schoolmaster and great barracuda; ontogenetic habitat shifts for these species were, at best, 'partial'. Unlike our results, they observed very little overlap in bluestriped grunt length-frequency with a high degree of separation of small and large individuals in mangrove and reef habitats, respectively (Negelkerken et al., 2000).

A third reason for little or no modal size progression from mangroves to reefs observed in our study may be related to sex-specific habitat preferences. Starck and Schroeder (1970) examined sex ratios of gray snapper collected from several inshore and offshore locations off South Florida. Some, but not all, of their collections suggested that female gray snapper, which attain larger sizes than males, predominate inshore, while the males, offshore. Clearly, comparative investigations of sex ratios, age structure, growth and mortality within and among inshore and offshore habitats are warranted as are tagging studies that quantify seasonal and ontogenetic movement by sex.

Densities of five taxa that occupy Biscayne Bay mangrove shorelines appear to be high relative to those reported for offshore habitats near Biscayne Bay or for the region (Table 3). For example, the densities of gray snapper, schoolmaster, bluestriped grunt, sailors choice and great barracuda estimated in our study range from four- to 120-fold higher than corresponding estimates for offshore reef habitats adjacent to Biscayne Bay. Our density estimates also exceed those reported for the entire Florida Keys reef tract (Bohnsack et al. 1999) and for mangrove and reef habitats near Bonaire (Negelkerken et al. 2000).

The general agreement of our gray snapper, schoolmaster, bluestriped grunt and great barracuda densities to those reported for mangrove shoreline habitats of Florida Bay (Table 3) lends credence to our density values and the visual technique employed.

Ideally, habitat-specific density values for a given species are combined with habitat area values to yield population abundance estimates. However, it is premature to attempt this for many Biscayne Bay fish populations, because of the conspicuous differences in gear performance, selectivity and practicality across all major fish habitats, or even across all mangrove habitat types, as mentioned earlier. A possible exception involves the use of block nets and fish poison (e.g., Thayer et al., 1987; Lorenz, 1999), but this technique is increasingly difficult to justify to fishery managers and to the public, especially when it comes to quantifying fish use of reef habitats. Without insight gained from species-specific, multiple-habitat, gear calibration studies, great caution must be exercised when combining and/or comparing fish density estimates derived using different methods within different habitats.

In general, mangroves have received little direct attention as potential contributors to southern Florida's reef fish resources which support a tourist industry and recreational and commercial fisheries valued in the billions of dollars (Bohnsack and Ault, 1996). Long-standing concerns about overfishing and habitat degradation resulted in the establishment of the Florida Keys National Marine Sanctuary (FKNMS) in 1990. Although the sanctuary encompasses a 9500 km² area that includes seagrass meadows, mangrove shorelines, mangrove islands and coral reef habitats, both commercial and recreational fishing are permitted within its boundaries. The effective area where fishing is prohibited within the sanctuary is limited to very small segments of the reef system and generally neglects adjacent shallow-water fish habitats, including mangroves. Based on the results of the present study and those of Ley et al. (1999) and Faunce et al. (2002), it would seem prudent to include mangroves habitats not only in future fishery resource monitoring efforts, but also in efforts to evaluate the impact of the ongoing Comprehensive Everglades Restoration Plan which will likely change salinity regimes within many of southern Florida's coastal bays and, thus, impact their ecological communities. We anticipate, therefore, that data presented herein will be of value as a 'baseline' from which to judge a variety of future changes to Biscayne Bay and its watershed.

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